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Bioturbation by stingrays at Ningaloo Reef, Western Australia

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Abstract

Stingrays are an important part of the biomass of the fishes in shallow coastal ecosystems, particularly in inter-reefal areas. In these habitats, they are considered keystone species – modifying physical and biological habitats through their foraging and predation. Here, we quantify the effects of bioturbation by rays on sand flats of Ningaloo Reef lagoon in Western Australia. We measured the daily length, breadth and depth of 108 feeding pits over three 7-day periods, created by stingrays (*Pastinachus atrus*, *Himantura* spp. *Taeniura lymma* and *Urogymnus asperrimus*) in Mangrove Bay. Additionally, an area of $\sim 1 \text{ km}^2$ of the lagoon at Coral Bay was mapped three times over 18 months, to record patterns of ray and pit presence. Over 21 days at Mangrove Bay, a total of 1.08 m^3 of sediment was excavated by rays, equating to a sediment wet weight of 760.8 kg, and 2.42% of the total area sampled, or 0.03% of the whole intertidal zone. We estimate that up to 42% of the soft sediments in our study area would be reworked by stingrays each year. Based on a model predicting the probability of pit presence over time, there was a 40% probability of ray pits persisting for 4 days before being filled in but only a 15% probability of a pit being present after 7 days. Changes in pit volume over time were static, providing evidence for secondary use. Our results imply that rays play an important ecological role creating sheltered habitats for other taxa in addition to the turnover of sediments.

Additional keywords: coral reef, Dasyatidae, feeding, pit, ray, soft-sediment, volume

Introduction

In the vast soft-sediment environments of the oceans, great numbers of species are bioturbators, creating, shaping and modifying the physical and biological properties of this habitat. Typically, this is done through behaviours such as feeding, digging or burrow formation by animals such as crabs (Eggleson *et al.* 1992), worms (Mermillod-Blondin & Lemoine 2010), sea cucumbers (Shiell & Knott 2010), urchins (Needham *et al.* 2010), dugongs (Nakaoka *et al.* 2002), turtles (Lazar *et al.* 2010), teleosts (Hall *et al.* 1990), elasmobranchs (Valentine *et al.* 1994) and even whales (Oliver & Slattery 1985).

Of the elasmobranchs, rays are one of the most obvious and ubiquitous fishes that act as bioturbators. This diverse group of cartilaginous fishes (over 600 living species) occupies marine ecosystems from the Arctic to the tropics (McEachran & Dunn 1998; McEachran & Fechhelm 1998; Frisk 2010). In shallow coastal and nearshore environments the Dasyatidae, or stingrays, are abundant and inhabit soft-sediment habitats ranging from mangroves to sandy shores and coral reefs (Snelson Jr *et al.* 1988; Gilliam & Sullivan 1993; Cartamil *et al.* 2003). The dorso-ventral compression of rays is thought to assist these animals to exploit shallow tidal areas for prey (Matern *et al.* 2000) where they feed by jetting water and beating pectoral fins to access infaunal and meiofaunal communities in soft sediment, a process of bioturbation that typically produces conspicuous feeding pits.

Rays frequently occur in large schools when feeding and migrating (Peterson *et al.* 2001), consequently they have the potential to exert a significant impact on both the

physical environment and biological communities that inhabit soft-sediment habitats. Feeding activity by rays on intertidal and subtidal sediments can significantly reduce benthic populations of harpacticoid copepods (Reidenauer & Thistle 1981), polychaetes and bivalves (Pridmore *et al.* 1990). Furthermore, rays have been implicated in severe damage to commercial shellfish operations (Smith & Merriner 1985; Blaylock 1989; Myers *et al.* 2007), as well as destroying seagrass beds (Orth 1975; Hovel & Lipcius 2001; Collins *et al.* 2007).

Despite the abundance and diversity of rays in both tropical and temperate shelf environments and their effects on benthic assemblages, there have been relatively few attempts to quantify patterns of bioturbation by these animals. Here, I quantify bioturbation by rays on soft sediments of a lagoon at Ningaloo Reef in Western Australia. Given that stingrays move in and out of shallow tidal areas on the reef in daily cycles (Cerutti-Pereya *unpub. data*), I hypothesised that new pits would form after each high tide that allowed access to feeding areas. If rays are highly efficient feeders, it would be expected that there should be little evidence for re-use of feeding pits and that pits should infill at relatively constant rates. I tested this hypothesis by surveying fixed quadrats in a feeding habitat and monitoring rates of infill of pits. Finally, given that large numbers of rays can inhabit shallow coastal zones, I examined the amount of sediment turned over by bioturbation by rays in a primary feeding habitat. In order to give a broader context to the impact of rays on sediments,

I surveyed ray pit formation over a large area of lagoon and reef (1 km²) that contained a variety of inter-reefal habitats.

Material and Methods

Study Locations

This study was conducted at two locations within the Ningaloo Reef Marine Park, Western Australia; Mangrove Bay (-21.9762, 113.9598) in the north and Coral Bay (-23.1335, 113.7703) in the lower section of the marine park (Figure 1). A marine protected area (sanctuary zone) in which all fishing is prohibited is in place at Mangrove Bay and extends for approximately 3 km from the shoreline to the outer reef and runs 4 km from north to south along the shore. Tidal range of Mangrove Bay during sampling was ≤ 1 m and the maximum water depth where pits were surveyed was 1.3 m. The sanctuary zone encompasses a small area of mangroves that are unique in this environment since they are found in very few other places within the Marine Park. My study site was the intertidal zone immediately adjacent to mangroves in the southern half of the bay. Within the bay, a large sand spit acts a tidal barrier forcing flooding tides round its head and then into the southern portion of the bay. Between the spit and the beach an area of approximately 100,000m² of muddy sands are exposed at low tide. The northern half of the intertidal zone of the bay consists of low-profile limestone reef with abundant macroalgae and very little sand.

At Coral Bay, I sampled an area of approximately 1 km² (1,000,000 m²) immediately south of the main boat launching facility, extending to the southern sanctuary zone

marker. The lagoon within this area was dominated by expanses of sand bordered on the seaward side by reef with high coral cover, which sheltered the lagoon from

current and swell. Maximum tidal range at Coral Bay was ≤ 1 m and the maximum depth of the Coral Bay lagoon sampled was 10 m.

Sampling

At Mangrove Bay, a total of 15 quadrats of 100 m² were monitored for seven days in each of November 2009, September 2010 and February 2011. Pits were measured after the first high tide each day in order to estimate rates of formation/infill every 24 hours. Quadrats were haphazardly placed in the area of muddy sediments to the south of the bay and within each quadrat, pits were identified, marked with a tent peg and high-visibility ribbon and positions recorded using a GPS. There are many bioturbating organisms that share this environment, so only pits that could be attributable to rays were included in the sampling and any depression or excavation which could not be unambiguously identified as due to a stingray was not included (Figure 2A).

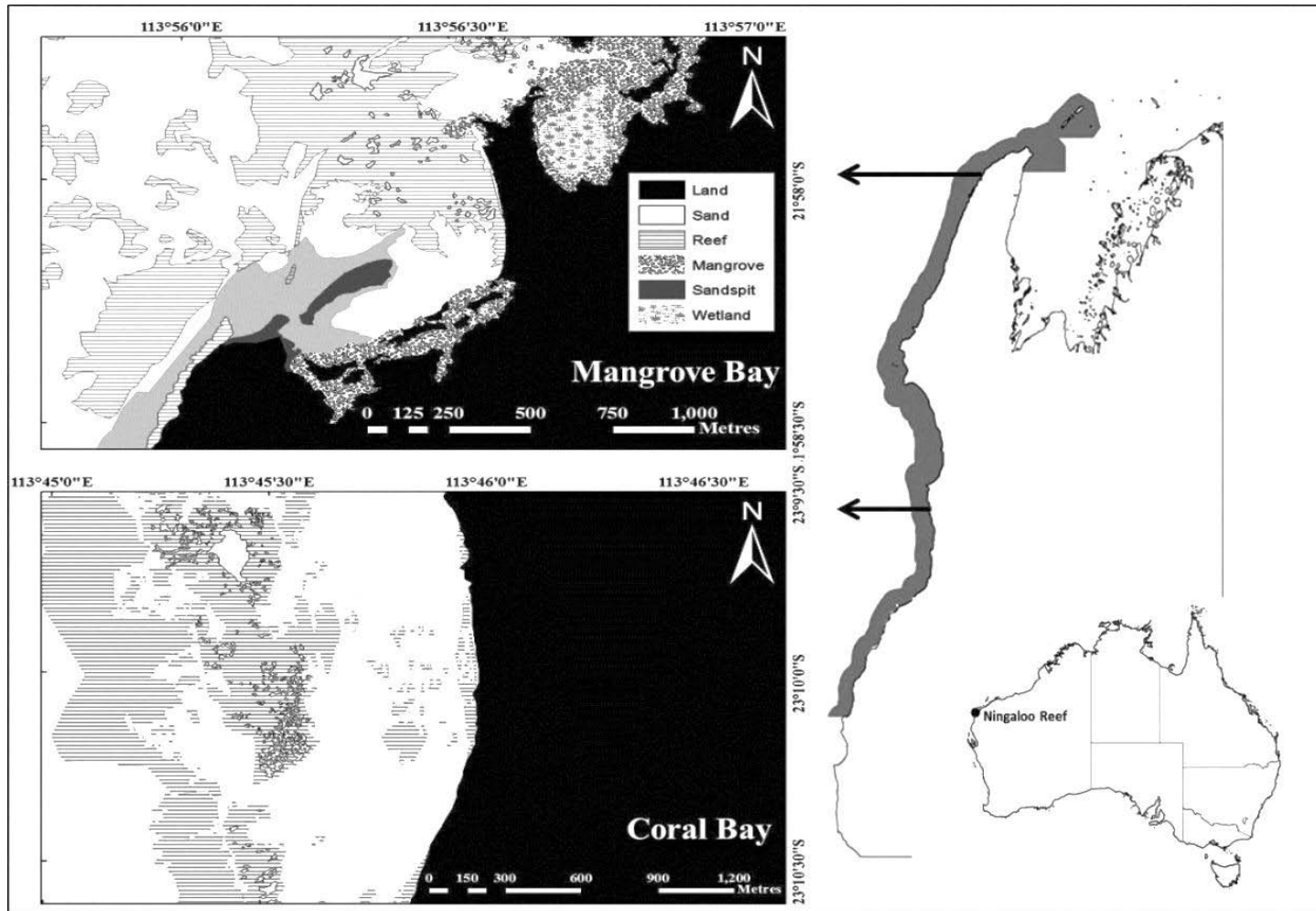


Figure 1: Ningaloo Reef Marine Park and the two study locations, Mangrove Bay and Coral Bay

The length, breadth and depth of pits was measured daily for a week or until the pits could no longer be discerned from surrounding sediment in order to test hypotheses relating to infill of pits and re-use by rays. Measurements were made using a tape measure and precision of measurements was approximately ± 1 cm for each pit. Any new pits were also marked and measured. All pits were examined for any secondary use by other fauna, such as crabs or juvenile fish (Figure 2B).

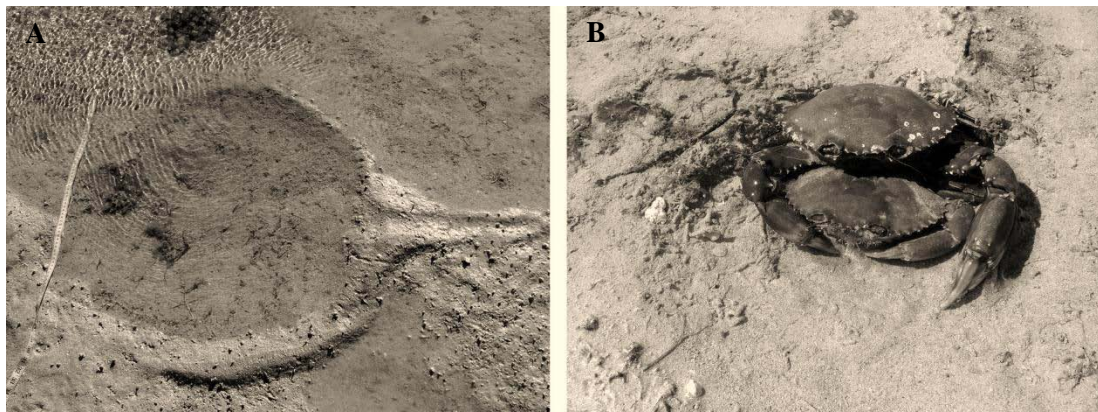


Figure 2: (A) New pit created by feeding ray, and (B) degraded pit with *Scylla serrata* occupying excavation

In Coral Bay, the lagoon habitat was surveyed for the presence of rays and pits in depths between 2 and 9 m. This was done in order to give a broader context to the impact of rays on sediments across a variety of soft-sediment habitats within the lagoon. Lagoon habitats were mapped and rays and pits recorded three times over this area in August 2009, August 2010 and February 2011. Observations were made by two snorkelers towed at 15 and 25 m behind a boat using manta boards (methods described by Miller & Müller 1999). Up to 15 – 20 transects spaced between 30 – 60 m apart were required to survey the entire area of 1 km². The variation in numbers of

transects were related to weather conditions and visibility. When there was lower visibility, transects were spaced closer than in good conditions, in order to ensure that observers covered the entire sampling area. The first observer would record the habitat immediately beneath them every 10 s in one of five categories (sand, coral reef, biogenic rubble, turf algae and seagrass), while the second would record ray pits and the presence of rays. The position of pits and rays were recorded using a GPS. The observer also recorded species identity and approximate size of all rays.

Analytical Procedures

To test the hypothesis regarding quantities of sediments being displaced by rays during activity, at Mangrove Bay I calculated the volume of empty pits by treating each ($n = 108$) as a semi-ellipsoid, using the equation:

$$- \quad (Lr \times Br \times Dr)/2;$$

where Lr = length radius, Br = breadth radius and Dr = depth radius. Wet weights of sediment for these volumes were extrapolated using the mean weight of 10, 1-cm³ samples of wet sediment from the same site. The intensity of disturbance created by rays feeding over the entire bay was determined by summing total pit area and dividing by the total sampling area to give a percentage of the total area disturbed. In order to determine the how long the pits persisted in the sediment at Mangrove Bay over the course of the seven day sampling period I fitted a generalised linear mixed model (GLMM) using a binomial distribution and a logit link function where the response variable was presence/absence of pits and the fixed, explanatory variable was time (day of the sampling period). I therefore modelled the probability of a pit

being present as a function of time. As individual pits were sampled repeatedly over time, individual pits were coded as a random effect to account for the temporal dependence structure between the observations. Pits were sampled over three years, thus pits were nested in years. Models were fit using the lme4 library in R: a Language and Environment for Statistical Computing (R development core team 2011) where the random effect was the individual pit nested in year. I used an information-theoretic approach to test for an effect of time by comparing Akaike's information criterion corrected for small samples (AIC_c) (Burnham & Anderson 2002) and the AIC_c weight ($wAIC_c$) of the slope model (probability of a pit being present \sim time + year/pit) to the intercept-only (null) model (probability of a pit being present \sim 1 + year/pit). The intercept-only model (or null model) is a model that does not contain any β (effects), except for an intercept. In this way I compared two models that were the same, except that one had the effect of interest (time) and one does not. The $wAIC_c$ is a measure of the models relative goodness of fit and varies from 0 (no support) to 1 (complete support) (Burnham & Anderson 2002).

Changes in the volume of pits over the sampling period were also examined using a linear mixed-effects approach. This analysis aimed to determine if rays were re-using a previously excavated pit, which would have created an increase in the volume of the pit over time, or pit volumes remaining static over time. All pits that were present for less than three days were removed from the analysis, as I could not fit a line to only two points. Pit volume was modelled as a function of day with the random effect pit nested in year and this model was compared to the null model as described above. Data were log transformed and the models fitted using the R library nlme.

Results

Mangrove Bay

A total of 108 pits were sampled over 21 days, equating to 2.42% of the area sampled and 0.031% of the entire soft-sediment habitat of the Mangrove Bay intertidal zone (Figure 3). The sediments excavated by rays during this time equated to 1.08 m³ with a wet weight of 760.8 kg, and the mean volume of pits from all years was 10,064 cm³ ($\pm 1,487$ SE). The numbers of pits varied among the three sampling times, but most notably in November 2009, when only 19 pits were found, accounting for 17.6% of the total number of pits found over the three sampling periods. In comparison, counts of pits in September 2010 and February 2011 accounted for 42% (n = 45) and 40% (n = 44) of total numbers respectively.

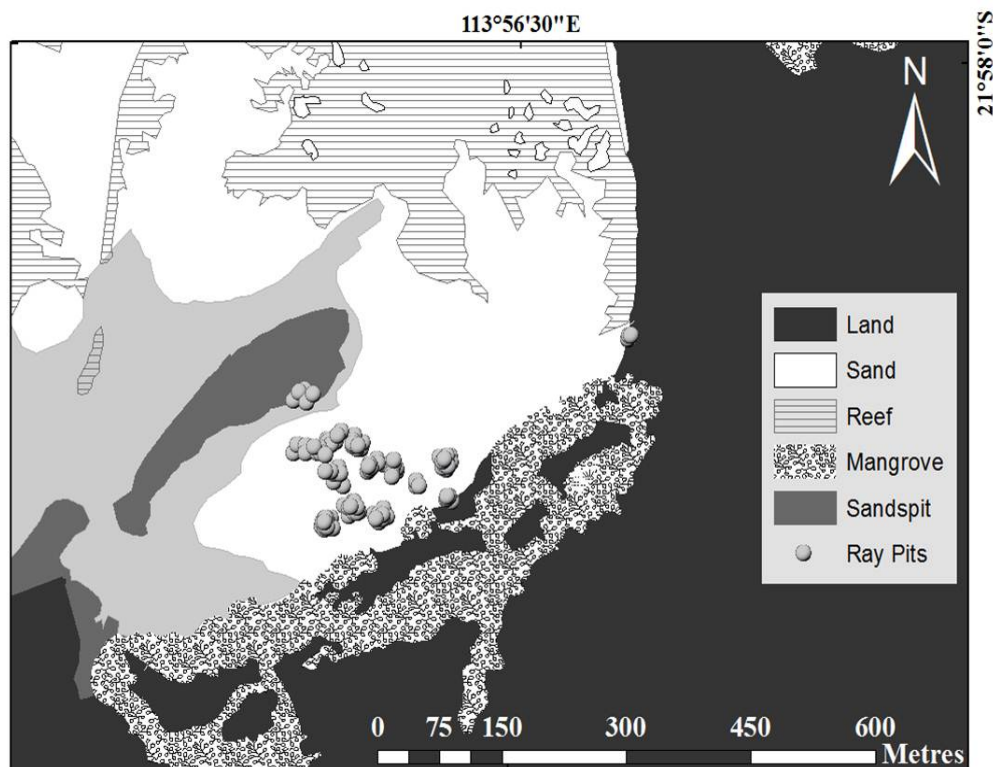


Figure 3: Mangrove Bay southern intertidal zone and position of all sampled pits

Pits ranged in volume from 334 cm³ - 100,577 cm³. Approximately 80% were relatively small (see Fig. S1 available as Supplementary Material to this paper). The estimated volume of pits also varied among sampling times, with mean volume in 2009 (21,939 cm³ \pm 4,774 SE) almost two and half times greater than in 2010 (8,782 cm³ \pm 2,507 SE) and three and half times greater than in 2011 (6,302 cm³ \pm 1,115 SE).

Longevity

The probability of a pit being present declined over the seven-day sampling period as indicated by 100% support for the model that included day as a factor ($wAIC = 1$) (Table 1). There was an 80% probability of an average pit being present on day one, with the probability of presence then rapidly declining to a low of 45% around day 4, to a low of 15% after seven days (Figure 4).

Table 1. Ranked general linear mixed effects models of the probability of a ray pit being present explained by day and random effects (pit nested in year), and the volume of ray pits explained by day and random effects (pit nested in year) LL, maximum log-likelihood; k , number of estimate model parameters; AIC_c , Akaike's Information Criterion for small samples; ΔAIC_c , change in AIC_c relative to the to ranked model ; $wAIC_c$, AIC_c weight

Model	LL	k	AIC_c	ΔAIC_c	$wAIC_c$
Presence ~ day + (1year/pit)	-398.80	4	805.65	0	1
Presence ~ 1 + (1year/pit)	-460.94	3	927.92	122.27	0
Volume ~ 1 + (1year/pit)	-303.89	4	615.84	0	0.91
Volume ~ day + (1year/pit)	-305.20	3	620.51	4.66	0.09

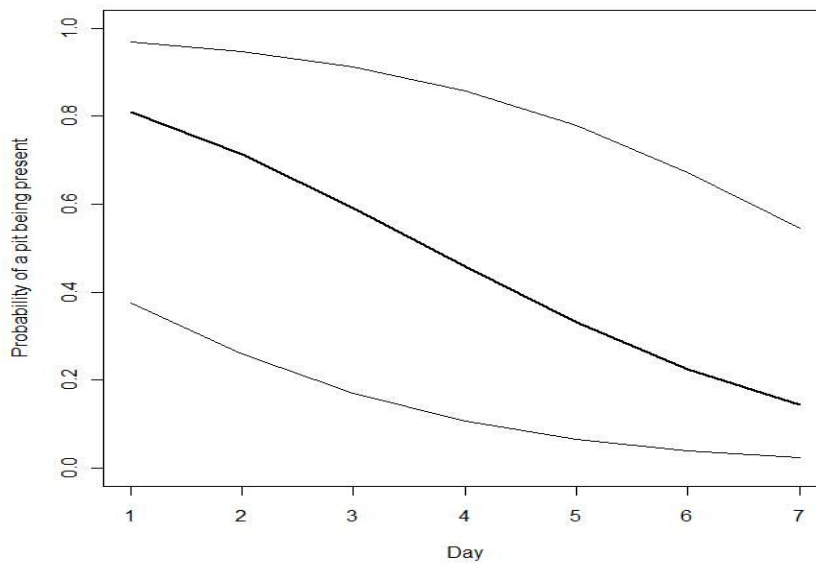


Figure 4: GLMM predicted probabilities of pit presence over time. The thick line in the middle represents the predicted probabilities for all pits and the lighter lines either side are 95% confidence intervals

Secondary use

There was little evidence for a relationship between volume of the pit and day of sampling (Figure 2) as the intercept only model (null) had majority support (91%) (Table 1). Thus, on average, pit volumes remained static over the sampling time, suggesting that re-use of pits by rays or other species was occurring. As the binomial model suggested that probability of a pit being present declined over the sampling period, it would have been reasonable to expect that the model for volume should also show a declining relationship. This did not occur, probably due to the inconsistent nature of the relationship between volume and day among years and pits, as can be seen in the individual plots of pits per year (Figure 5 and Supp. Figures 3 and 4). Overall, a decline between volume and time occurred in 48% of pits, with the remaining pits showing a

static (22%) or increasing (30%) volume. In 2009, 35% of pits increased in volume over 7 d ($n = 17$) (Figure 5); in 2010, 46% of pits increased in volume, ($n = 11$) (Supp. Figure 3) and in 2011, 17% of pits increased in volume ($n = 18$) (Supp. Figure 4). Of the 22% of pits that did not change in volume throughout the period of sampling, 12% occurred in 2009 (Figure 5); 36% in 2010 (Supp. Figure 3) and 27% in 2011 (Supp. Figure 4). These results are evidence for re-use of the pits either by rays or other organisms.

2009

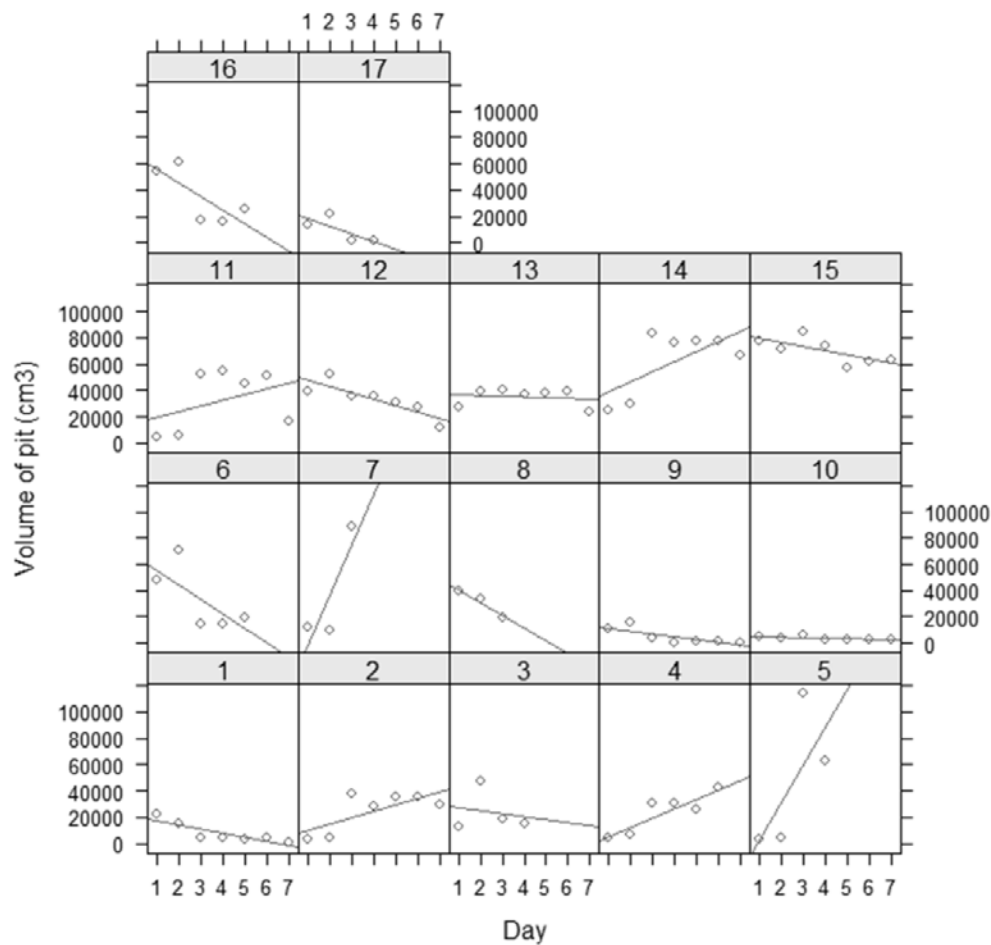


Figure 5: Linear relationships between day of sampling and volume of each of the pits sampled from November 2009 that were present for three days or more

Rays were not directly observed re-using pits; however observations did indicate secondary use by other taxa in all new pits formed during the study. Small fish were the most common occupants at low tide (90% of all pits), where pits remained full of water. Adult fish were occasionally seen in larger pits ($> 10,000 \text{ cm}^3$, $n = 7$); however, over half of these were dead or dying, probably as a result of attacks by sea birds. Invertebrates such as gastropods (*Nerita* sp.) were found in 87% of all pits.

Accumulation of detrital material and seaweed was common in every pit examined at low tide, and this in turn created a potential refuge for organisms such as crabs. The mud crab *Scylla serrata* was abundant at Mangrove Bay and 25% of pits had at least one adult inhabiting it on day 1 when sampling began; while newly formed pits were occupied by this species in 10% of cases within 24 hours.

Coral Bay

The lagoon at Coral Bay was dominated by sand (48%) and coral reef (36%).

Biogenic rubble (6%) and turf algae (10%) were present in all years; however seagrass (< 1%) was only documented in February 2011 at the far southern end of the map boundary. Over the three sampling periods, a total of 20 rays from six species and 37 ray pits were observed, with the highest number of both rays (n = 9) and pits (n = 14) recorded in the first sampling session during August 2009. A total of 11 pits and 6 rays were recorded in August 2010 and 12 pits and 5 rays recorded in February 2011. Of the 37 pits, 92% were recorded in sand and 8% were recorded in sand where turf algae was also present. Six species of ray were sighted during the sampling:

Urogymnus asperrimus (n = 5), *Neotrygon kuhlii* (n = 4), *Taeniura lymma* (n = 1),

Himantura uarnak (n = 3), *Pastinachus atrus* (n = 6) and *Taeniura meyeni*

(n = 1). Over half (55%) of all rays were buried in sand and of these, all were found within 2 m of coral, or some form of structure. *T. lymma*, *N.kuhlii* and *U. asperrimus* were all found immediately adjacent to reef, buried and inactive. *T.meyeni* was observed swimming in mid-water, as were two *P. atrus*. All *H. uarnak* and the remaining *P.atrus* were found feeding or resting in open sandy habitats.

Discussion

Sediment removal

This study shows that rays can be significant agents of bioturbation in the intertidal area of a coral reef ecosystem. Ray feeding pits over seven days disturbed an average of 2.42% of an area of intertidal habitat of 500 m². When extrapolated to a year, this would result in sediment turnover of 42% of the entire intertidal soft-sediment habitat (~ 42,000 m²) to a mean depth of 5.6 cm. This estimate is comparable to an earlier study of bioturbation by rays (*Dasyatis americana*, *D. sabina* and *Gymnura micrura*) in a temperate estuary in South Carolina, where 30% (6000 m²) of the study area was covered in ray pits during a July sampling period (Grant 1981). Larger volumes of sediment were reportedly re-worked by *Myliobatis californica* and *Urolophus halleri* at Bahia La Choya in Mexico (Myrick & Flessa 1996). Their study found that these two species of ray were overturning sediments at an average rate of 1.01 m³/m²/year, with > 100 new pits formed every 24 hours. In comparison, rays at Mangrove Bay overturned sediments at the much lower rate of 0.167m³/m²/year.

Comparable Taxa

It is difficult to compare estimates of bioturbation by rays with those of other large vertebrates in coral reef systems because very few studies exist. The potential for bioturbation by animals such as the dugong (*Dugong dugon*) is well recognised, with numerous studies of the frequency and effects of feeding scars on benthic habitats and biological communities (Heinsohn & Birch 1972; Nakaoka *et al.* 2002; Skilleter *et al.* 2007). However, there has been no attempt to quantify the volume of material or turnover rates of sediment moved by these animals. In contrast, bioturbation by invertebrate taxa, notably callianassid shrimps, has been documented extensively in coral reef systems (Branch & Pringle 1987; Murphy & Kremer 1992; Tudhope & Scoffin 1984). These shrimps are deep burrowers and the volume of sediment that

they are capable of processing is immense. Myrick and Flessa (1996) estimated that these shrimps turned over sediment on a sand flat in Mexico at an average of $0.56 \text{ m}^3 / \text{m}^2 / \text{year}$; a rate 3.5 times greater than the $0.167 \text{ m}^3 / \text{m}^2 / \text{year}$ I recorded for rays at Mangrove Bay. Similarly, Riddle (1988) found that the physical effects of powerful cyclones on soft sediments were quickly erased (within 6 weeks) by the action of callianassid shrimps in the lagoons on the Great Barrier Reef.

Mangrove Bay vs. Coral Bay

This study examined an intertidal sandflat that was adjacent to an important habitat for juvenile rays and other elasmobranchs. Acoustic tracking studies have shown that rays, particularly juveniles and adult females are present in this subtidal habitat year-round and that this area may function as a nursery for a variety of ray species (Cerutti-Pereya *unpub. data*). Thus, the rates of bioturbation I recorded in this area may not be representative of the wider lagoon of Ningaloo Reef. My surveys of the southern lagoon suggest that this is the case. Sampling over $1,500 \text{ m}^2$ of the sandflat at Mangrove Bay recorded 108 feeding pits, while manta tows over 1 km^2 of the lagoon at Coral Bay recorded only 37 pits during three surveys. However, it is likely that the greater current flows and ‘clean’ sand in the lagoon at Coral Bay result in much faster disintegration of feeding pits at this locality than at Mangrove Bay. A total of six species of ray were sighted by my surveys at Coral Bay. These species

are common throughout Ningaloo Reef (Stevens *et al.* 2009) and it is likely that they are responsible for creating the feeding pits at Mangrove Bay. At high tide these rays move into the intertidal, presumably to feed although these shallow waters may also provide a refuge from predation. It is probable that I under-estimated numbers of rays

in the lagoon of Coral Bay, since the smaller species tend to be cryptic, either burying themselves in sediment (e.g. *Neotrygon kuhlii*) or hiding under reef outcrops (e.g. *Taeniura lymma*).

Longevity

The longevity of ray pits has received little attention, despite the possibility that they create micro-habitats that may differ from surrounding areas in carbon transport, nutrient regeneration, sediment stability and decomposition processes (Austen *et al.* 1999). The formation of ray feeding pits may create bio-geochemical gradients that in low-energy environments may take many days or weeks to infill, which may account for some of the unexplained variation in the structure and abundance of benthic communities on smaller (cm – m) spatial scales (Zajac *et al.* 2003). As expected, I found a negative relationship between pit presence and time, as pits were not permanent structures and were subject to infilling. These model results showed that there was a reduced probability of an average pit remaining after 4 days (~ 40%) and at the end of the 7-day sampling period there was on average only a 15% probability of a pit still being present. My analysis of the change in pit volume over time, however, did not always follow the same negative trend. Over the seven days of monitoring, only 48% of pits in-filled while the rest remained static or increased in volume. This latter result is

evidence for reuse of pits by other taxa, some of which are known bioturbators, such as crabs. The slow disintegration of pits at Mangrove Bay was also probably related to the protection of the habitat from strong wave action and current flow. Given that they are common and relatively persistent structures in the soft sediment, it is likely that pits play an important role in shaping population distributions and structures of

infaunal communities (Zajac *et al.* 2003). It has been proposed that losses of bioturbating organisms could impair marine ecosystem function (Thrush & Dayton 2002; Lohrer *et al.* 2004) and yet despite this, few data are available on pit formation by rays. Biological effects of ray pits are well documented (e.g. VanBlaricom 1982, Cross & Curran 2000) and typically demonstrate that infaunal communities are removed by ray feeding, which is followed by a rapid re-colonisation of pits by ostracods and amphipods (VanBlaricom 1982). On a microbial level, the creation of pits can allow oxygen to penetrate deeper into sediments, extending the zone of nitrification (Gilbert *et al.* 1995) and even affecting the nitrogen cycle compromising functions of specific bacterial groups (Kogure & Wada 2005). These responses highlight the importance of pit formation in the ecology of marine soft sediment environments and any loss of rays in these habitats may lead to changes in lower trophic and biogeochemical levels.

In conclusion, this study has quantified the persistence of ray pits, rates of infilling and sediment turnover rates in an intertidal area of a coral reef ecosystem. In doing so, I have demonstrated that bioturbation by rays can be a significant functional process in coastal and nearshore environments and may be critical to physical,

biological and chemical processes at least in some intertidal habitats. Despite 42% of the soft sediment habitat of Mangrove Bay being re-worked on an annual basis, this rate of turnover was much lower than recorded by earlier studies of bioturbators, which have tended to focus on temperate marine ecosystems. Furthermore, bioturbation may be relatively trivial when considered in the context of sediment turnover by tidal and wave action (Grant 1981). This implies that ray pit formation

might be most relevant to biological communities on micro (cm) and meso (10s m) rather than meta (100s m – km) scales (Zajac 2004). Future work will examine the prey and selectivity of ray feeding at Ningaloo Reef and its effects on infaunal communities.

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Supplementary Material

Fig. S1. Volume frequency of all pits sampled at Mangrove Bay

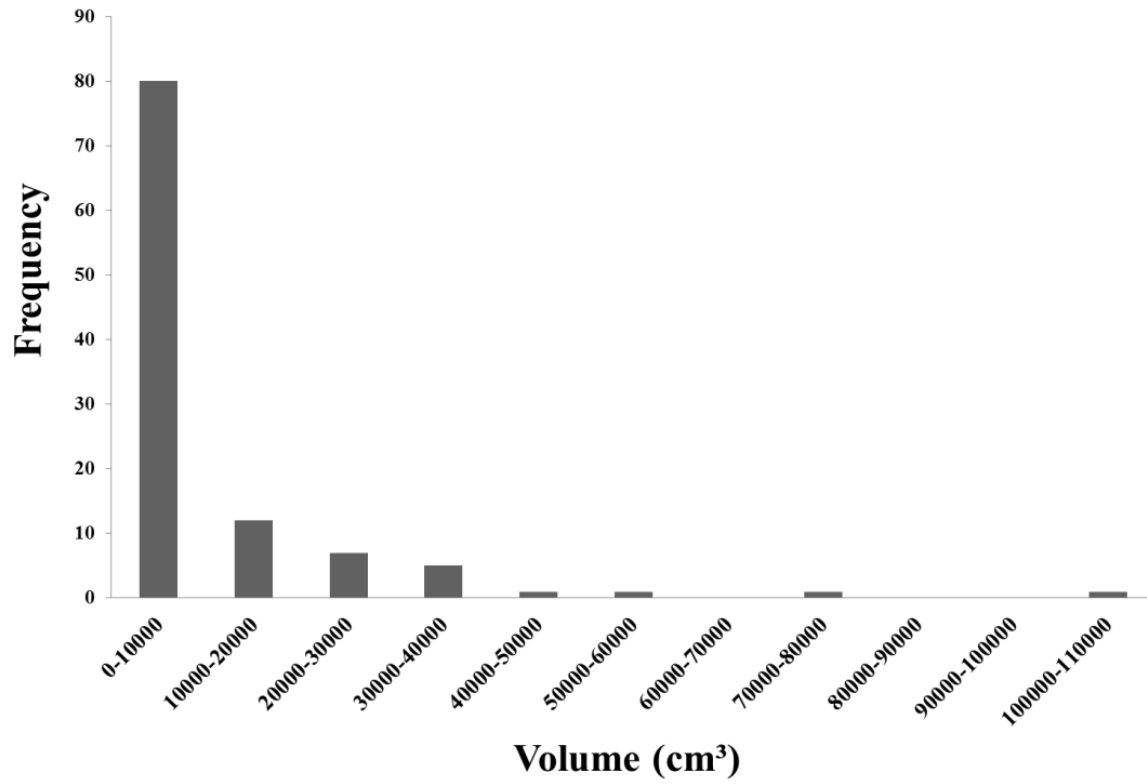


Fig. S2. The log-transformed volume of all pits sampled from 2009, 2010 and 2011 that were present for three days or more is plotted on the y-axis, against day of sampling on the x-axis. The un-transformed values are plotted on the opposite y-axis and the fitted line for the population of pits obtained by the linear mixed effects model is shown.

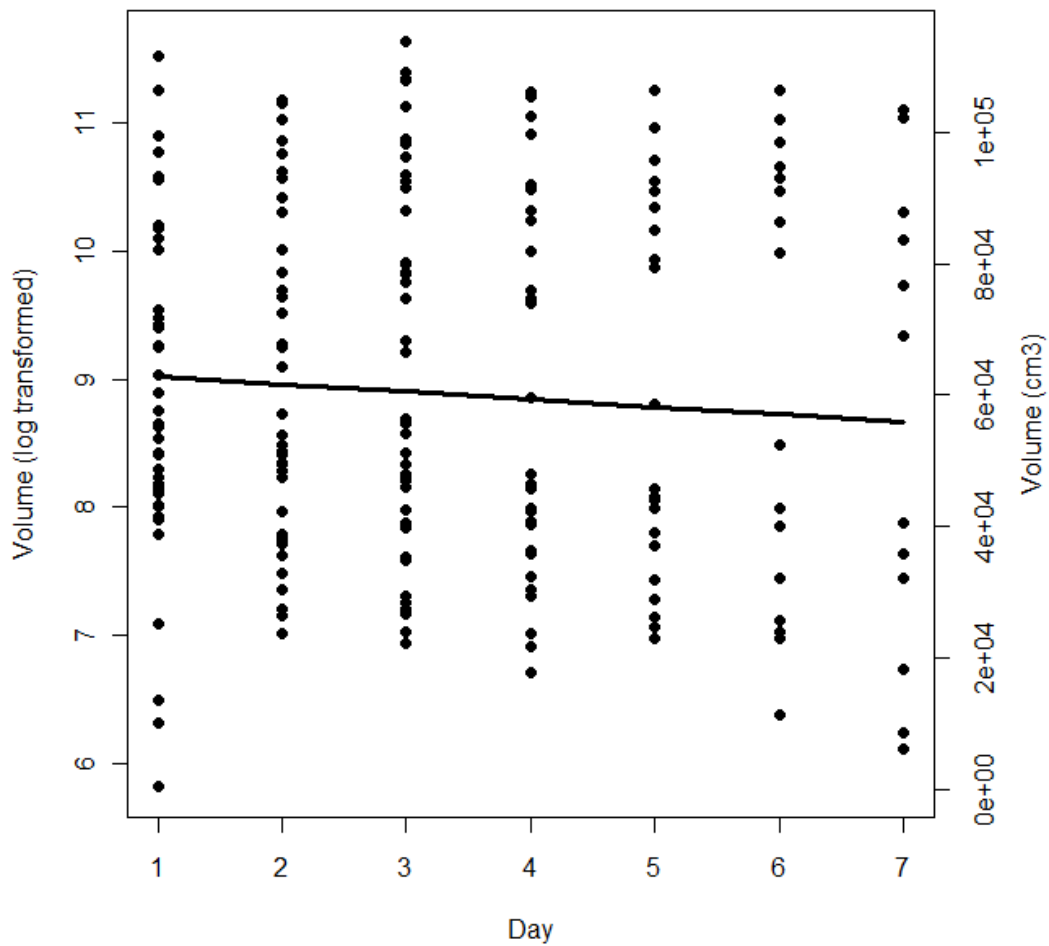


Fig. S3. Linear relationships between day of sampling and volume of each of the pits sampled from September 2010 that were present for three days or more.

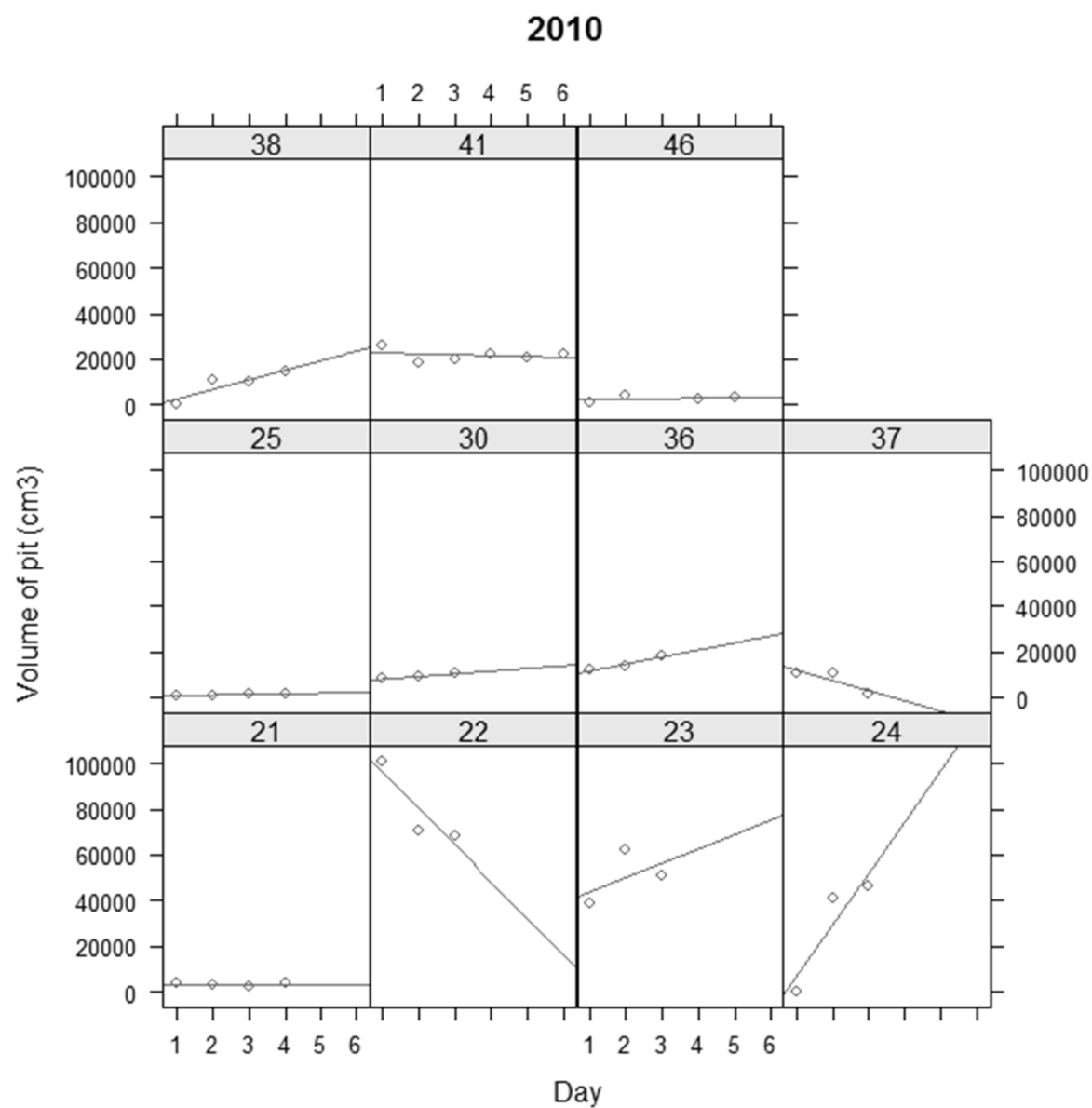


Fig. S4. Linear relationships between day of sampling and volume of each of the pits sampled from February 2011 that were present for three days or more.

